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REPORT

Coral bleaching impacts from back-to-back 2015–2016 thermal anomalies in the remote central Indian Ocean

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Abstract Studying scleractinian coral bleaching and recovery dynamics in remote, isolated reef systems offers an opportunity to examine impacts of global reef stressors in the absence of local human threats. Reefs in the Chagos Archipelago, central Indian Ocean, suffered severe bleaching and mortality in 2015 following a 7.5 maximum degree heating weeks (DHWs) thermal anomaly, causing a 60% coral cover decrease from 30% cover in 2012 to 12% in April 2016. Mortality was taxon specific, with *Porites* becoming the dominant coral genus post-bleaching because of an 86% decline in *Acropora* from 14 to 2% cover. Spatial heterogeneity in *Acropora* mortality across the Archipelago was significantly negatively correlated with variation in DHWs and with chlorophyll-a concentrations. In 2016, a 17.6 maximum DHWs thermal anomaly caused further damage, with 68% of remaining corals bleaching in May 2016, and coral cover further declining by 29% at Peros Banhos Atoll (northern Chagos Archipelago) from 14% in March 2016 to 10% in April 2017. We therefore document back-to-back coral bleaching and mortality events for two successive years in the remote central Indian Ocean. Our results indicate lower coral mortality in 2016 than 2015 despite a more severe thermal anomaly event in 2016. This could be caused by increased thermal resistance and resilience within corals surviving the 2015 thermal anomaly; however, high bleaching prevalence in 2016 suggests there remained a high sensitivity to bleaching. Similar coral mortality and community change were seen in the Chagos Archipelago following the 1998 global bleaching event, from which recovery took 10 yr. This relatively rapid recovery suggests high reef resiliency and indicates that the Archipelago's lack of local disturbances will increase the probability that the reefs will again recover over time. However, as the return time between thermal anomaly events becomes shorter, this ability to recover will become increasingly compromised.

Keywords Coral bleaching · Chagos archipelago · Coral mortality · British Indian Ocean Territory · BIOT · Coral community composition

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Introduction

Coral reefs are experiencing increasing levels of both chronic and acute disturbances, which can cause coral mortality and alter reef community composition, impacting their ability to accrete carbonate and keep pace with sea-level rise (Oliver et al. 2018; Perry et al. 2018). Coral bleaching events associated with thermal anomalies are acute disturbances recognised as the primary global challenge to the persistence of coral reefs (Darling and Cote 2018). Thermal anomalies associated with the El Niño Southern Oscillation (ENSO) are occurring with increasing frequency and severity, driven by anthropogenic climate change (Hughes et al. 2003; Veron et al. 2009), with two sequential events occurring on many reefs between 2014 and 2017 globally (Eakin et al. 2017; Hughes et al. 2017). In particular, the 2016 thermal anomaly surpassed the previous global-scale warming event of 1998 in intensity and duration (Eakin et al. 2017; Oliver et al. 2018).

Coral reef futures now predominantly depend on how scleractinian corals respond to repeated warming events, and if they can adapt to altered climatic conditions. There are several mechanisms by which this may occur: (1) at the level of the coral holobiont, through physiological adaptation, genetic variation, altered *Symbiodinium* or microbiome composition (Rowan 2004; Roche et al. 2018); (2) through changes in the dominant taxa comprising reefs (Hughes et al. 2003; Berumen and Pratchett 2006); (3) via spatial shifts where reef communities either colonise new areas or remain in limited environmental 'refuge' locations (e.g. Camp et al. 2017). Gathering data on the effects of recurrent bleaching events on coral reefs is critical in assessing the strength and spatial extent of these proposed adaptation mechanisms. The prevalence of such mechanisms, and their relationship with key reef physical and ecological characteristics will determine how coral reef functioning is altered under future climate change, and which reefs are most likely to display resistance or recovery (Holling 1973).

Bleaching is a natural stress response of corals to changes in environmental conditions, including increases in sea temperature (Brown 1997). Bleaching can be divided into two parts: (1) the initial response where corals expel *Symbiodinium* and (2) the longer-term effect which may be either coral tissue recovery or mortality. The proportion of colonies that bleach represents coral sensitivity, and is a means to assess varying temporal and spatial bleaching impact. Yet in many cases bleaching does not result in coral mortality (Suggett and Smith 2011). Understanding of the relationship between coral bleaching and subsequent mortality is also evolving. Recent evidence suggests that the response to repeated bleaching events, and the ability of coral taxa to acquire resistance to bleaching events, may vary between global ocean regions: reports from the Great Barrier Reef (GBR) of a lack of an adaptive response (Hughes et al. 2017) contrast with those from Kenya indicating a reduction in the severity of response from 1998 to 2016 (McClanahan 2017). There is evidence that recent pre-exposure of corals to higher temperatures can promote resistance to bleaching (Grottoli et al. 2014). However, research on the GBR has shown that future predicted increases in local temperatures of as little at 0.5 °C may result in this protective mechanism being lost (Ainsworth et al. 2016). At a regional scale, the degree of bleaching response appears spatially consistent between events, with areas that are less susceptible retaining this characteristic in subsequent events (Penin 2013).

Bleaching, and mortality or recovery patterns commonly operate against the background of localised natural and anthropogenic disturbances such as nutrient enrichment, overfishing, and direct human pressure. The nature and extent to which these stressors interact in the processes of bleaching and coral mortality are uncertain (Welle et al. 2017); however, there is some evidence that reef stressors act synergistically (Veron et al. 2009). For example, a reduction in herbivore fish abundance due to overfishing increases algal growth, hence reducing the ability of a reef to recover from bleaching because algal species begin to outcompete recovering corals (Hughes et al. 2007).

Thermal resilience in individual coral colonies is comprised of two key processes: (1) resistance to bleaching and (2) subsequent recovery from bleaching (Mumby et al. 2007; Darling and Cote 2018; Roche et al. 2018). A wide range of factors have been associated with resilience to heat stress, often termed 'resilience indicators' (Obura and Grimsditch 2009; Rowlands et al. 2012; Graham et al. 2015). For instance, higher reef structural complexity has been shown to increase recovery potential (Graham et al. 2015). Wave energy (exposure) increases vertical mixing and associated surface cooling of the water column (Obura and Grimsditch 2009), and some coral hosts are able to increase heterotrophic feeding rates to obtain their daily metabolic energy requirements during bleaching (Grottoli et al. 2006). It is challenging to disentangle the impacts of such factors on reef resilience to thermal anomalies from the effects of local anthropogenic disturbances. It is essential, therefore, to study bleaching impacts on reefs with minimal local human disturbance to enable the effects of global bleaching to be disentangled from interactions with local-scale threats.

The Chagos Archipelago, British Indian Ocean Territory, located in the central Indian Ocean offers an opportunity to examine bleaching dynamics with minimal local human disturbance such as no agricultural runoff, industrial pollution and reef fisheries. The majority of the Chagos

Archipelago has been uninhabited since the 1970s with the exception of a US military base on one atoll, Diego Garcia, which has strict environmental regulations (Sheppard et al. 2012). As a result, fishing pressure has largely been absent from the Chagos Archipelago since the 1970s, though some illegal harvesting of sea cucumbers (Price et al. 2009) and shark poaching activities are reported (Graham et al. 2010). In 2010, the UK government designated the British Indian Ocean Territory (BIOT) exclusive economic zone (EEZ) a 640,000 km^2 marine protected area (MPA), which incorporated the Chagos Archipelago (Sheppard et al. 2012).

In this study, we investigate the effects of the 2015 and 2016 thermal events on reefs surrounding uninhabited Chagos Archipelago atolls. We present data on bleaching patterns and subsequent coral mortality occurring over two successive bleaching events. We also analyse spatial variation in coral mortality across the Archipelago primarily attributed to the 2015 and 2016 bleaching events and use remote sensing data to investigate whether coral mortality is correlated with SSTs, wave exposure, and/or plankton abundance. In the Chagos Archipelago, there is higher productivity on reefs surrounding islands with high seabird populations, whilst reefs surrounding islands with invasive rats, and hence lower seabird populations, have lower productivity (Graham et al. 2018; Ferretti et al. 2018). Nutrient input from seabird guano has been associated with increased plankton populations (McCauley et al. 2012), which could affect coral heterotrophic feeding rates. Wave exposure around the Archipelago differs substantially depending on the orientations of the reefs, with the south-east trade winds blowing from May to September and the north-west trade winds from October to March (Perry et al. 2015). Also the South Equatorial Current (SEC) flows east–west and reverses for a few months a year (Obura 2012). Our results provide crucial insights into the effects of the 2015 and 2016 thermal stress on coral reefs in remote, isolated oceanic islands in the central Indian Ocean.

Materials and methods

Remote sensing data

To obtain time series of thermal stress in each survey location, NOAA Coral Reef Watch (2013) Degree Heating Week (DHW) products were sourced at daily 5 km resolution in NetCDF format. DHW indicates for a given pixel location the accumulation of thermal hotspots greater than 1 °C relative to the long term climatological mean SST of the hottest month experienced in that pixel. DHW is calculated for a 12-week period preceding a given date. The 5 km gridded thermal data products do not resolve fully to the shallow water reef face, nor island landmasses, and may be flagged as land. Where this corresponded with the location of one of our survey sites (Fig. 1), the value of the nearest pixel with valid SST data was used.

Surface chlorophyll-a mean values (mg m^{-3}) were extracted for survey sites using Google Earth Engine (Gorelick et al. 2017) for 1 March–15 June 2015 and 15 February–15 April 2016 from the 500 m resolution Ocean Color SMI: Standard Mapped Image MODIS Aqua Data (NASA Goddard Space Flight Center 2018). Net wave energy (kW m^{-1}) was extracted for survey site coordinates from the Marine Socio-Environmental Covariates database which has calculated mean wave energy to at least 50 km^2 spatial resolution from 3-hour temporal resolution for a span of 31 yr (Yeager et al. 2017).

Benthic surveys and image analysis

Benthic transects were surveyed at 12 survey sites from four atolls—Peros Banhos Atoll, Salomon Atoll, Great Chagos Bank (GCB) Atoll, and Egmont Atoll—across the Chagos Archipelago (Fig. 1) in April 2012 and 2013 and April 2016. Three 30 m long benthic transects were surveyed per site. In 2012, an Olympus Xz-1 digital camera was used to take a planar benthic image every 0.5 m along each transect from approximately 0.3 m height. In 2016 continuous planar video transects were recorded with a Hero4 GoPro holding the camera approximately 0.3 m above the benthos. All transects were along a continuous transect tape laid parallel to the shoreline at approximately 8–10 m depth with at least 5 m separating adjacent transects. Three replicate transects were planned for each survey site, but at one survey site (South Brother within GCB) only two transects were conducted. At one site, Moresby, data were not collected in April 2012 and so were excluded from some of the analysis (figure legends indicate sample size).

In addition to April 2012 and April 2016 surveys, at three sites in north-western Peros Banhos Atoll (Ile Diamant Seaward, Ile Diamant Lagoon, Moresby; Fig. 1), additional benthic transects were also undertaken in March 2016, May 2016 and April 2017 (three transects per site per survey) following the method outlined for April 2016. March 2014 benthic data were also obtained for Ile Diamant Seaward and Moresby from Samoilys et al. (2018). This allowed for a short time-series tracking the bleaching event between 2012 and 2017.

For video transects, still images were extracted every 0.5 m using VLC software (version 2.2.3; http://www.videolan.org/vlc). Coral Point Count (CPC; Kohler and Gill 2006) was used to analyse images with ten points randomly placed over each image. The benthic taxa or substrate under each point was identified and recorded. Scleractinian

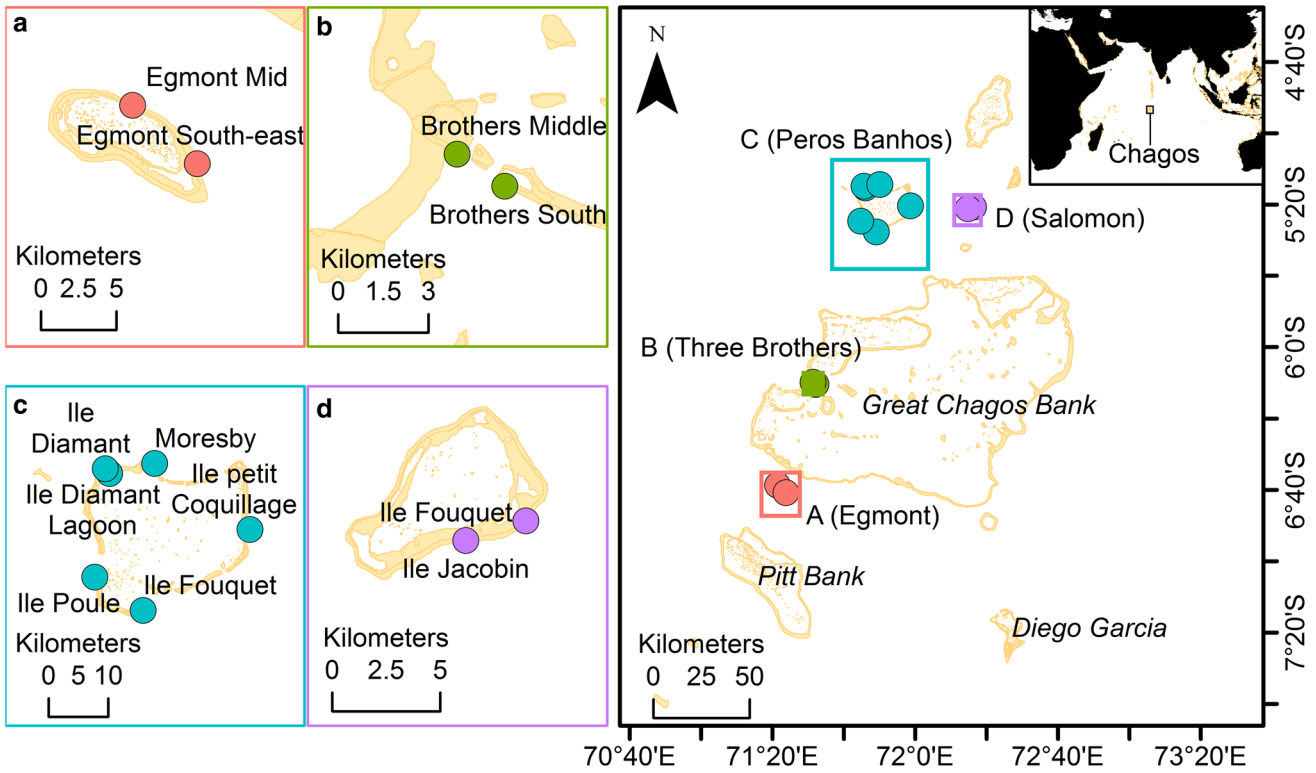

Fig. 1 Map of the Chagos Archipelago with the 12 survey sites across the four atolls illustrated, accompanied by close-up maps of survey sites at **a** Egmont Atoll, **b** brothers islands of the Great Chagos Bank, **c** Peros Banhos Atoll, **d** Salomon Atoll. Note colours correspond to colour schemes in Figs. 3 and 5

corals were identified to genus where possible or family level if not, the growth form and condition of the coral were also recorded. Coral condition was classified as bleached, diseased, dead or healthy. Where identification was not possible, the coral was recorded as unidentifiable. All raw data are available online at https://doi.org/10.6084/m9.figshare.7063712. (Raw data will be released at this DOI upon publication of the paper.)

Statistical analysis

Summary statistics were calculated for each survey site to illustrate change in benthic cover between April 2012 and April 2016 for total live coral cover, non-living substrate, algae (macro-algae, calcareous and turf algae), and key scleractinian genera including *Acropora*, massive *Porites* and *Pocillopora*. Wilcoxon signed-rank tests were used to evaluate differences in each benthic cover category between survey years.

Generalised linear models (GLMs) were used to test for correlations between the percentage change in total coral cover/*Acropora* cover/massive *Porites* cover from 2012 to April 2016 with three environmental variables: SST (maximum DHWs), chlorophyll-a (mg m^{-3}), and net wave energy (kW m^{-1}). Because the dependent variables represent proportions, the logit-link function and binomial family function were used. A GLM was fitted for each dependent variable to the predictor environmental variables and their interactions and then evaluated by comparing the AIC for each model. All models that demonstrated overdispersion (residual deviance higher/lower than degrees of freedom) were fitted with the quasi-family function to introduce a dispersion parameter and obtain a quasi-likelihood estimate (Crawley 2005). Model significance was assessed using *F*-values or Chi-squared values depending on the nature of the dependent variable. The amount of deviance accounted for by the model was calculated using the modEvA package (Barbosa et al. 2014).

One-way repeated measure ANOVAs were used to evaluate the changes through time in the proportion of bleached corals (as a proportion of the total coral cover) and the proportion of healthy coral cover (as a proportion of the total benthic cover) at the three survey sites in Peros Banhos with the time-series 2012–2017. Data were rank-transformed before performing the one-way repeated measure ANOVAs using the nlme package (Pinheiro et al. 2018) because the data are not normally distributed. Data analysis was undertaken in R version 1.1.383 (R Development Core Team 2017) and MATLAB version 2018a,

with results plotted using the ggplot2 package (Wickham 2016).

Results

Chagos Archipelago reef thermal stress

The geographic distribution and magnitude of thermal stress in Chagos differed in 2015 compared to 2016 (Fig. 2). In 2015 the Chagos Archipelago experienced a maximum of 7.5 DHW, at the north-western tip of the Great Chagos Bank. Here, conditions were at NOAA Bleaching Alert (https://coralreefwatch.noaa.gov/satellite/methodology/methodology.php) Level 1 (greater or equal to 4 DHW and less than 8 DHW), where bleaching is considered likely, for a total of 11 weeks between 22 April and 7 July and did not reach Alert Level 2 (greater than 8 DHW), where mortality is considered likely. The thermal anomalies were more extreme in 2016 across the entire archipelago, but greatest in the south-west. Here a maximum of 17.6 DHW was recoded at Pitt Bank. Between 18 March and 21 July, conditions at Pitt Bank were at NOAA Alert Level 1 for 5 weeks and at Level 2 for 13 weeks.

2012–2016 Benthic trends

Live healthy coral cover declined significantly between 2012 and 2016 from 30 ± 2% (Mean ± 1 SE) to 12 ± 1%, representing a 60% decrease, across the Chagos Archipelago at the 8–10 m depth band ($V = 292$, $p < 0.001$; Table 1 and Fig. 3a). South Brother Island, west GCB, suffered the largest decline from 43 ± 1 to 7 ± 1% coral cover, representing an 84% decrease. The eastern side of Egmont Atoll was the only site where coral cover increased from 11 ± 1% in 2012 to 14 ± 1% in 2016, representing a 27% increase, but this was not significant ($V = 0$, $p > 0.05$) (Fig. 3).

Acropora and massive *Porites* together were the most abundant coral genera in Chagos in 2012 comprising 47% and 34% of all coral cover, respectively. *Acropora* cover declined significantly between 2012 and 2016 from 14 ± 2 to 2 ± 1% of the benthos, representing an 86% decrease ($V = 297$, $p < 0.001$; Fig. 3). Hence, in 2016 *Acropora* comprised approximately 14% of coral composition. Cover of *Acropora* declined in all sites surveyed, with ten of the survey sites exhibiting < 2% *Acropora* cover in 2016, including Ile Jacobin and Ile Fouquet (east side of Salomon Atoll) declining to below detectable levels. Ile Diamant lagoon and seaward sites (north-west Peros Banhos) were the only two sites with > 5% *Acropora* in April 2016. Massive *Porites* showed a less uniform pattern across the

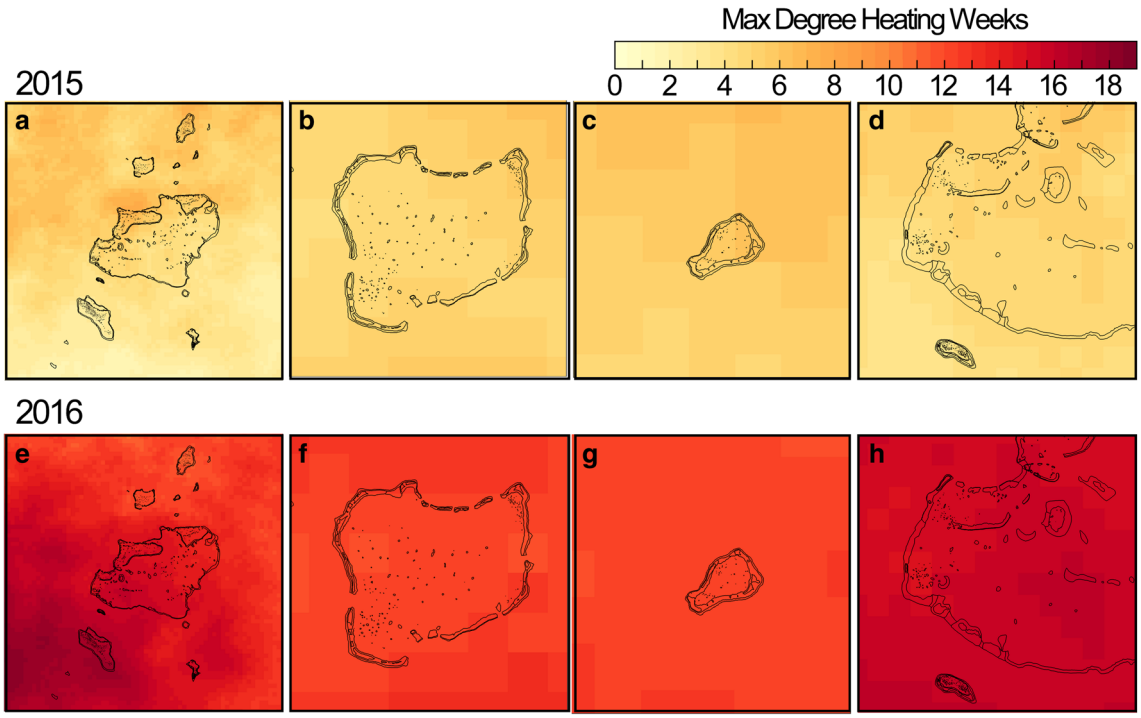

Fig. 2 Heat maps from across the Chagos Archipelago from 1 January–31 December 2015 and 2016 illustrating **a**–**d** the maximum DHWs in 2015, and **e**–**h** the maximum DHWs in 2016. Maps show: **a**, **e** whole Chagos Archipelago, **b**, **f** Peros Banhos Atoll, **c**, **g** Salomon Atoll, and **d**, **h** the western GCB and Egmont Atoll

Table 1 Mean changes in per cent benthic cover across the Chagos Archipelago from 2012 to 2016 and results of the Wilcoxon signed-rank test to evaluate the difference in benthic cover between April 2012 and April 2016 across the Archipelago

Benthic category	2012 mean (%) ± SE	2016 mean (%) ± SE	Wilcoxon test statistic (V)	*p* value
Mean healthy live coral cover	30 ± 2	12 ± 1	292	< 0.001*
Mean healthy *Acropora*	14 ± 2	2 ± 1	297	< 0.001*
Mean healthy *Porites*	10 ± 1	8 ± 1	206.5	0.110
Mean healthy *Pocillopora*	2 ± 1	0.2 ± 0.3	276	< 0.001*
Mean algae cover	1 ± 0.5	4 ± 0.9	26	0.002*
Mean non-living substrate	54 ± 2	68 ± 2	43	0.001*

*Represents a significant result

Archipelago with six survey sites showing a decline, whilst five survey sites showed an increase (Fig. 3). Overall, the trend in massive *Porites* cover across the Chagos Archipelago from 10 ± 1% of the benthos in 2012 to 8 ± 1% in 2016 was non-significant ($V = 206.5$, $p = 0.110$; Fig. 3). By 2016, because of the *Acropora* decline, massive *Porites* became the most dominant coral taxon comprising 65% of the live coral composition.

Although *Pocillopora* was not a dominant coral genus in 2012, it still declined significantly. *Pocillopora* declined from 2 ± 1% of the benthos to < 1% across the Archipelago ($V = 276$, $p < 0.001$; Fig. 3). Ile Diamant lagoon (north-west Peros Banhos) and Ile Fouquet and Ile Jacobin (south-east Salomon) all declined to below detectable levels of *Pocillopora* cover by 2016 (Fig. 3).

Algae cover across the Archipelago (macro-algae, calcareous and turf algae combined) showed a significant increase from 1 to 4% of the benthos, representing a 75% increase ($V = 26$, $p = 0.002$; Fig. 3). Macro-algae cover decreased from 1 to < 1% of the benthos, accounting for 99% of the total algae cover in 2012 but only 4% of total algae cover in 2016. Substantial heterogeneity was observed within sites and between algae lifeforms, particularly in 2016, with one transect (Ile Petite Coquillage) containing 21% total algal cover in 2016. However, algal cover was well below 10% of the benthos in the majority of transects. Across the Archipelago, there was also a significant increase in non-living substrate ($V = 43$, $p = 0.001$; Fig. 3), concurrent with the decline in coral cover.

Spatial heterogeneity in coral cover change across the Archipelago 2012–2016

Spatial heterogeneity in coral cover change across the Archipelago (April 2012 to April 2016) was not significantly correlated with 2015 maximum DHWs (*GLM*, $F = < 1$, $p = 0.994$; Fig. 4a), wave energy (*GLM*, $F = 0.161$, p value = 0.702), nor chlorophyll-a concentration (*GLM*, $F = 0.161$, $p = 0.7$). Mean chlorophyll-a concentrations ranged from 0.125 mg m^{-3} at Ile Fouquet in Salomon Atoll to 0.275 mg m^{-3} at South Brothers in GCB (Fig. S1). Mean wave energy ranged from 0.38 kW m^{-1} at Ile Diamant lagoon in Peros Banhos Atoll to 33.74 kW m^{-1} at the south-east site of Egmont Atoll (Fig. S1). DHWs explained < 1% of the spatial variation in coral cover change across the survey sites, whilst wave energy and chlorophyll-a both explained 2% of the variation.

Spatial heterogeneity across the Archipelago in *Acropora* cover change was significantly correlated with maximum DHWs (*GLM*, $\chi^2 = 22.59$, $p = <0.05$; Fig. 4c), and chlorophyll-a concentration (*GLM*, $\chi^2 = 6.582$, $p = <0.01$) but not with wave energy (*GLM*, $\chi^2 = 28.378$, $p = 0.209$). Our GLMs find that maximum DHW patterns explained 19% of the variation in change in *Acropora* cover (Fig. 4c), chlorophyll-a concentration explained 15% and wave energy explained 5%. Spatial heterogeneity in massive *Porites* change in cover was not significantly correlated with maximum DHWs (*GLM*, $\chi^2 = 0.14$, $p = 0.708$; Fig. 4e), wave energy (*GLM*, $\chi^2 = 1.85$, $p = 0.173$), or chlorophyll-a concentration (*GLM*, $\chi^2 = 1.182$, $p = 0.277$), but there was a significant interaction between maximum DHWs, mean wave energy and chlorophyll-a concentration (*GLM*, $\chi^2 = 6.583$, $p = 0.01$). This significant interaction may be a result of the effect of wave energy on water mixing which would likely impact sea surface temperatures and chlorophyll-a concentrations. DHWs explained < 1% of the *Porites* heterogeneity across the survey sites, with wave energy explaining 14% and chlorophyll-a explaining < 2% of the heterogeneity.

2016–2017 Further coral bleaching and mortality

We surveyed three sites in north-west Peros Banhos Atoll in April 2012, March, April, and May 2016, and April 2017. The change in the relative abundance of bleached coral colonies (as a proportion of total coral cover) through

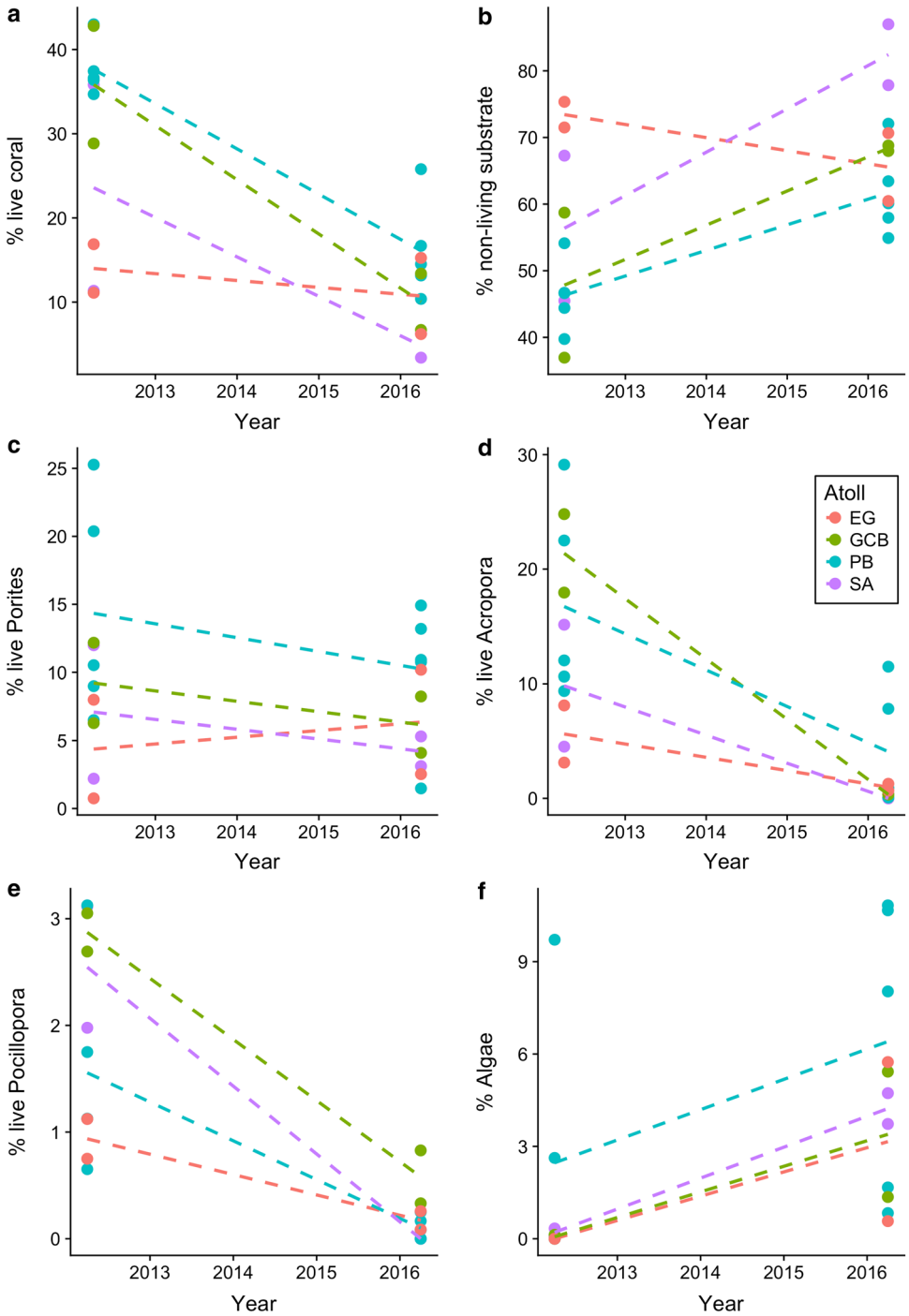

Fig. 3 The change in benthic composition from April 2012 to April 2016 across all survey sites, summarised by atoll (EG = Egmont, GCB = Great Chagos Bank, PB = Peros Banhos, SA = Salomon) in: **a** total live healthy coral cover, **b** non-living substrate, **c** live healthy massive *Porites* sp. coverage, **d** live healthy *Acropora* sp. coverage, **e** live healthy *Pocillopora* sp. coverage, **f** algae coverage. 'Live coral' refers to non-bleached live coral

time was significant ($F = 8.03$, $p = 0.016$), with bleached colonies observed during all surveys in 2016 and 2017. We identified an increase in the proportion of bleached corals from March 2016 (11 ± 4%) through April 2016 (24 ± 9%) to May 2016 (68 ± 6%; Fig. 5a, Table 2). This correlates with the increase in maximum degree heating weeks (DHWs) for the area from 4 DHWs on 22 March 2016 to 15 DHWs on 15th May 2016, the day of our final 2016 assessment (Fig. 5). Surveys conducted in April 2017 showed the proportion of bleached colonies to be 10 ± 6%. Whilst this detailed time series is restricted to the three north-west Peros Banhos sites, in 2016 bleaching appeared to be widespread in Chagos. Our surveys of 11 sites in April 2016, before peak DHWs were reached for 2016, identified 4 ± 2% bleached coral cover.

The trend in healthy coral cover (as a proportion of total benthic cover) through time was also significant ($F = 16.63$, $p = 0.003$). Healthy coral cover reduced from

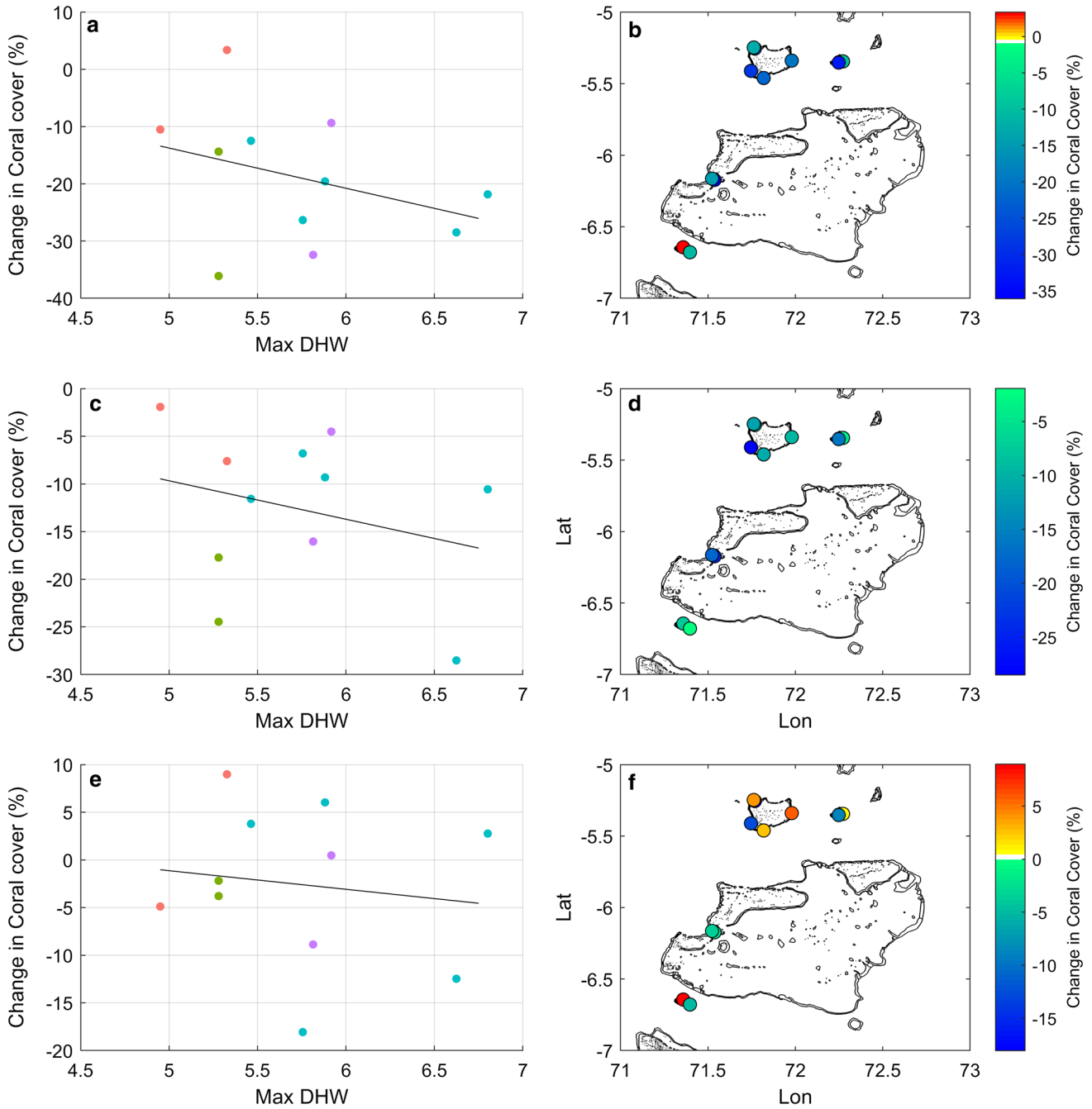

Fig. 4 Relationship between maximum DHWs (March 2012–April 2016) and the change in coral cover (April 2012–April 2016) for each site. (**a**, **b**) Total coral cover, (**c**, **d**) *Acropora* sp. cover, (**e**, **f**) *Porites* sp. cover. For **a**, **c**, **e** colours correspond to atolls as illustrated in Fig. 1 (red = Egmont, blue = Peros Banhos, purple = Salomon, green = GCB). For (**b**, **d**, **f**), maps illustrate the spatial variation in coral cover change between April 2012–April 2016

14 ± 3% in March 2016 to a low of 5 ± 1% in May 2016, before increasing to 10 ± 2% in April 2017 (Table 2 and Fig. 5b), suggesting some recovery from the 2016 bleaching but an overall decline of 29%.

Discussion

Our results show that during the period 2012–2017 there was significant widespread severe loss of hard coral cover in the Chagos Archipelago, which occurred in at least two distinct events correlated with peaks in DHWs in 2015 and 2016. During this time, hard coral communities on reefs

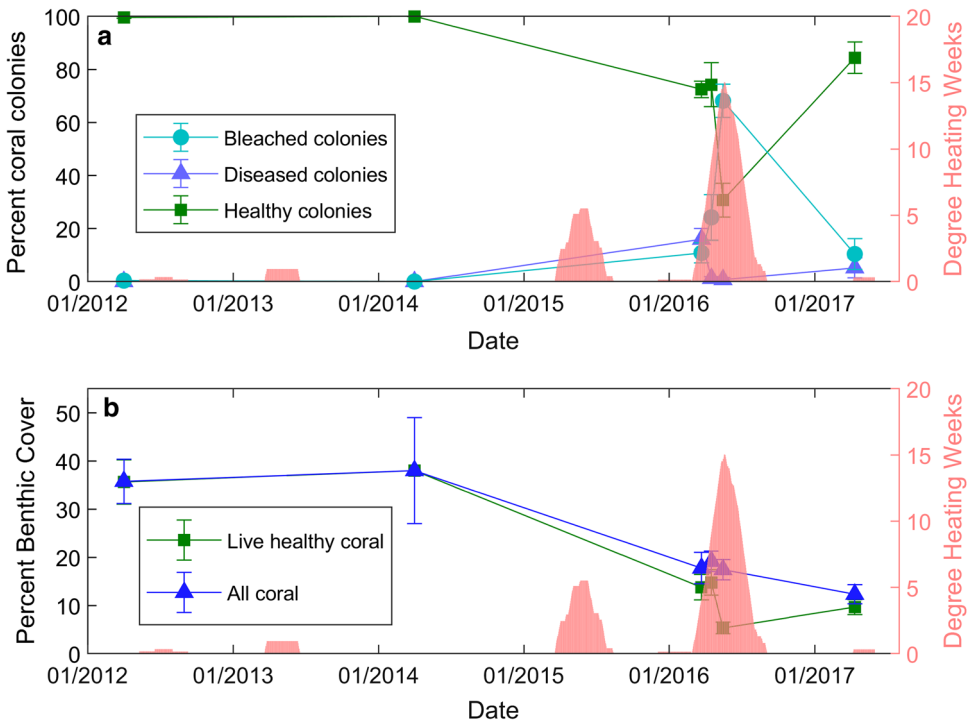

Fig. 5 Trends in coral health and cover and associated degree heating weeks (DHWs) for three sites in north-west Peros Banhos. Peaks show the DHWs corresponding to temperature anomalies in 2015 and 2016 for the three sites (n = 3). **a** The lines represent cover of bleached, diseased, and healthy coral as a percentage of total coral cover, and **b** live healthy coral cover and all coral (healthy, bleached, and diseased) as a percentage of total benthic cover, in April 2012, April 2014, March 2016, April 2016, May 2016, and April 2017

Table 2 Trends in the mean bleached coral as proportion of live coral cover, and in mean healthy corals as a proportion of the benthic cover at three sites at Peros Banhos Atoll in March, April, and May 2016 and April 2017. Results of the one-way repeated measure ANOVAs to evaluate changes in the two benthic categories through time

Benthic category	March 2016 mean (%) ± SE	April 2016 mean (%) ± SE	May 2016 mean (%) ± SE	April 2017 mean (%) ± SE	ANOVA (F statistic)	p value
Mean bleached corals as % of live coral	11 ± 4	24 ± 9	68 ± 6	10 ± 6	8.03	0.016*
Mean healthy corals as % of the benthos	14 ± 3	15 ± 2	5 ± 1	10 ± 2	16.63	0.003*

*Represents a significant result

within the Archipelago shifted from being *Acropora*-dominated to massive *Porites*-dominated, because of high *Acropora* mortality. Our results are consistent with the global impacts of coral bleaching reported over the same period (Eakin et al. 2017, Hughes et al. 2018, Claar et al. 2018) in response to increases in SSTs as a result of an ENSO climatic event which originated in the Pacific in 2014 (Couch et al. 2017).

The significant correlation between spatial variation in *Acropora* decline and DHWs provides evidence that the peaks in water temperature in March–June 2015 and 2016 were the predominant cause of the recorded coral mortality. No other severe peaks in DHWs were recorded in Chagos between our 2012 baseline data and early 2015 (Fig. 5). Surveys conducted in the Chagos Archipelago in April 2015 recorded > 40% healthy coral cover, whilst surveys conducted in May 2015 observed approximately 30% of corals bleached (Sheppard et al. 2017). Our April 2016 surveys represent the first follow up surveys following this 2015 DHW peak. Whilst Sheppard et al. (2017) identified that the 2015–2016 bleaching event had caused widespread coral mortality, our study now suggests this mortality was partitioned into two distinctive but back-to-back bleaching events. In north-west Peros Banhos, the greatest coral cover loss (36% in 2012 to 14% in 2016) was caused by thermal stress in 2015 (6 DHWs), followed by a subsequent smaller loss (14% in 2016 to 10% in 2017) caused by the more severe thermal stress (15 DHWs) in 2016 (Fig. 6). We surmise that this pattern is a result of thermal stress in 2015 causing a die-off of corals with little to no thermal adaptation or ability to acclimatise. Therefore, the remaining coral population exposed to thermal stress in 2016 was a more thermally resilient population, to some degree.

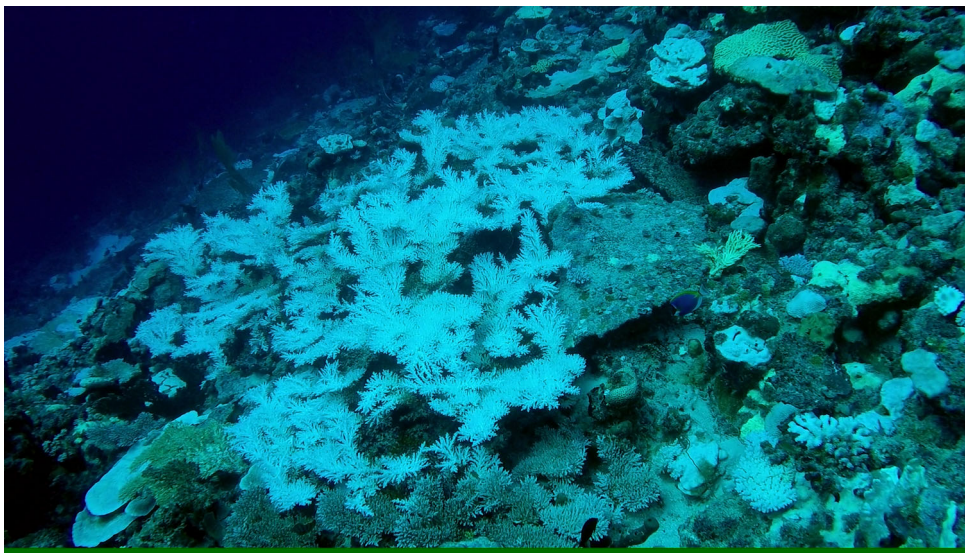

Fig. 6 Extensively bleached *Acropora* spp. at Ile Diamant Seaward site, Peros Banhos Atoll, in May 2016

Mechanisms behind thermal resilience need further investigation but may include thermal adaptations through physiological and genetic variation of the coral hosts, the dinoflagellate algae and associated microorganisms, and/or through community change (Roche et al. 2018). At two fully protected Kenyan marine reserves McClanahan (2017) reported a reduction in sensitivity to bleaching in coral taxa, including *Acropora* and *Porites*, between two bleaching events (1998 and 2016). A similar pattern has also been reported in Moorea between bleaching events in 2002 and 2007 (Penin 2013). In contrast, on the Great Barrier Reef exposure to bleaching in 1998 and 2002 did not lessen the severity of bleaching in 2016 (Hughes et al. 2017). Within the Chagos Archipelago, a high proportion of corals bleached in 2016 (72%), but it is not possible to quantitatively compare this to the proportion of bleaching in 2015 or in previous years to assess whether past exposure has lessened sensitivity to bleaching. However, there was less coral mortality following the 2016 temperature anomaly, compared to coral mortality levels recorded after the 2015 temperature anomaly. This is possibly due to past exposure to temperature anomalies in 2015 creating a more thermally resilient coral population. Coral community change is a likely mechanism behind this reduction in mortality because a significant proportion of the more thermally susceptible taxa (Darling et al. 2012), e.g. *Acropora* and *Pocillopora*, had suffered high mortality rates after the 2015 bleaching event. Nevertheless, the increases in DHWs (17.6 max DHWs in south-west) in 2016 did cause bleaching and subsequent mortality, albeit at lower levels.

The pattern of bleaching and mortality in the Chagos Archipelago can be compared with other locations in the Indian Ocean, where the most severe bleaching impacts appear to have occurred in 2016 (McClanahan 2017). For example, in the Maldives, a similar oceanic atoll reef system in the northern Indian Ocean, the greatest thermal stress was also experienced by reefs during May 2016 (Perry and Morgan 2017a). This resulted in mean coral cover declines from 26% in January 2016 to 6% in September 2016 (Perry and Morgan 2017a). In the Chagos Archipelago, mean coral cover levels in April 2016 were already down to 12% before 2016 bleaching began, likely a result of the 2015 bleaching event, although high levels of background mortality and disease within tabular *Acropora* were consistently observed following the 1998 bleaching event (Pratchett et al. 2010, 2013). Similar proportions of corals in north-west Peros Banhos Atoll (Chagos Archipelago) bleached in 2016 (68% in May 2016) as in the Maldives during the peak of bleaching (77% in May–June 2016; Ibrahim et al. 2017). Following the Maldivian reef bleaching, in March 2017 many sub-massive and compact branched colonies that had originally survived began to show partial mortality (Perry and Morgan 2017b).

The spatial heterogeneity in coral cover decline across the four atolls in the Chagos Archipelago which was not attributed to spatial variation in DHWs may be due to other interacting environmental factors and the corals' physiological and genetic characteristics. An individual coral colony's susceptibility to stress and bleaching is known to be highly variable as a result of eco-physiological and genetic adaptations (Coles and Brown 2003; Weis 2008). Environmental variables also play a part, and here we tested whether wave energy or plankton availability (using chlorophyll-a as a proxy) were drivers of spatial variation in coral decline. Chlorophyll-a concentrations were significantly directly correlated with the spatial heterogeneity in *Acropora* cover decline. Spatial variability in plankton

availability as a food source for heterotrophic feeding has been shown to explain variation in coral trophic ecology (Fox et al. 2018), and some coral species can increase heterotrophic feeding to meet metabolic needs (Grottoli et al. 2006). However, rather than suggesting that higher plankton availability may lead to higher coral survivorship during bleaching, our results suggest that chlorophyll-a concentrations are correlated with an increase in coral decline—although the heterogeneity in chlorophyll-a concentrations is low (0.125–0.274 mg m^{-3}) across the Archipelago and hence may not be meaningful. In contrast, wave energy was not found to be a significant driver of spatial heterogeneity in coral cover decline. Increases in wave energy can result in water column mixing and cooling and flushing of the benthic boundary layer (Obura and Grimsditch 2009), but its effect depends on the depth of mixing resulting from the waves and the depth of the thermocline. It is probable that these variables would need to be more closely measured through in-water instrumentation at a closer proximity to each reef than through existing remote sensing methods. Interestingly Safaie et al. (2018) recently found high-frequency temperature variability (i.e. daily temperature range) to be the largest predictor of bleaching prevalence globally. Within the Chagos Archipelago, localised daily temperature plunges of between 5 and 7 °C at frequencies of 1–4 d, thought to be driven by upwelling of cooler water as a result of internal wave formation, have been recorded at some locations (Sheppard 2009) and may further explain the spatially heterogeneous patterns in coral mortality.

Whilst this study documents geographically widespread severe declines in coral cover on reefs at approximately 10 m depth, bleaching mortality was not equal across depth. Our quantitative diver surveys were limited to shallow reefs because of the remoteness of the Chagos Archipelago, but during April 2016 and April 2017 brief observations were also made to 25 m depth. On reefs below approximately 15 m, coral mortality from bleaching was reduced (Sheppard et al. 2017). During April 2016, remote-operated vehicle surveys were also conducted in the Chagos Archipelago of upper mesophotic coral ecosystems (MCEs) between 30 and 60 m depth (Andradi-Brown et al. 2019). Although there is a limited historical baseline to compare these deeper surveys to, these surveys suggested that at least some MCE sites may have been minimally affected by the 2015 bleaching event and so maintained crucial biodiversity and fish habitat. For example, MCE reefs at Ile Anglaise, Salmon Atoll, in the 35–45 m depth range, had close to 100% live *Pachyseris speciosa* cover, with no evidence of bleaching when surveyed in April 2016 (Andradi-Brown et al. 2019).

Reefs of the Chagos Archipelago recovered from severe bleaching following the 1998 global coral bleaching event with coral cover back to pre-1998 levels by 2010 and a canopy cover of coral observed by 2006 (Sheppard et al. 2012). The SSTs in 1998 rose by a mean of 1 °C over 2 months, and coral cover around the Archipelago fell from 50–70% (1996) to ~ 10% on shallow (5–10 m) outer reefs (1999) (Sheppard 1999). Massive *Porites* accounted for approximately 80% of this remaining live coral cover in 1999, whilst *Acropora* table corals were recorded as nearly completely absent (Sheppard 1999). This level of coral cover post-bleaching and the composition of *Acropora* and *Porites* are very similar to the results we report from the 2015 and 2016 bleaching. After the mortality caused by the 1998 bleaching event signs of recovery were observed from surveys 3 yr after the event, with coral recruits recorded at densities of 28 m^2, the highest recorded globally at the time (Sheppard 2002; Harris and Sheppard 2008). Sheppard et al. (2017) report lower densities of coral recruits in April 2017, 1 yr on from the 2016 bleaching, but the levels are still high in comparison to records from other locations (Cowburn et al. 2018; Turner et al. 2018). Also, modelling studies have predicted good vertical and horizontal larval connectivity in the Chagos Archipelago, which would facilitate coral recruitment and subsequent reef recovery (Riegl and Piller 2003). Mean algae cover remained low in 2016 surveys at 4%, consistent with a high herbivorous fish biomass (Graham et al. 2013) reducing algal growth and allowing coral recruits the space to recolonise the reef.

In summary, coral mortality attributed mainly to the 2015/2016 bleaching events has been severe in the Chagos Archipelago, and similar to that reported in many other locations globally (Hughes et al. 2017; Eakin et al. 2017; Couch et al. 2017; Claar et al. 2018). This shows that the remoteness of the Archipelago and its protected nature, which safeguards the reefs from most direct human impacts, does not provide it with resistance to bleaching and subsequent mortality. However, the Chagos Archipelago recovered well from the 1998 bleaching event, when coral mortality rates were similar to those seen in back-to-back 2015/2016 event reported here. This evidence of historic resilience plus reasonable coral recruitment levels, high coral cover in MCEs and high herbivorous fish biomass make for an optimistic outlook for recovery within the Archipelago. However, the longer-term outlook for reefs of the Chagos Archipelago depends on their ability to maintain resilience to the increasingly frequent and severe thermal anomalies predicted as a consequence of accelerating global climate change.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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